

JEM 393

HERBIVORY POTENTIAL OF POSTLARVAL BROWN SHRIMP ASSOCIATED WITH SALT MARSHES

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Abstract: Laboratory feeding experiments were used to study the herbivory potential of postlarval brown shrimp (*Penaeus aztecus* Ives). Plant materials fed to shrimp included *Skeletonema costatum* (Greville) Cleve, *Isochrysis* sp., *Spartina* detritus, and *Spartina* epiphytes. A total of 16 treatments were derived from all possible combinations of the four materials. After 16 days the greatest increases in length and weight occurred in those treatments containing *Skeletonema costatum* (*Skeletonema* group) followed by *Spartina* epiphytes exclusive of the presence of *Skeletonema* (epiphyte group). Shrimp growth did not occur in beakers with (1) no food, (2) *Isochrysis* sp. or *Spartina* detritus alone or (3) *Isochrysis* and detritus in combination (*Isochrysis*–detritus–no food group). Ecdysis occurred in all treatments, except where no food was present, including those in which there was no measurable growth. Survival and growth were significantly higher in the *Skeletonema* and epiphyte groups compared to the *Isochrysis*–detritus–no food group. These results indicate that planktonic diatoms, such as *Skeletonema*, and epiphytes of *Spartina* are potential sources of nutrition for postlarval *Penaeus aztecus* in *Spartina* marshes.

Key words: *Penaeus aztecus*; herbivory; growth; survival; postlarvae; *Spartina* salt marshes

INTRODUCTION

The general life-cycle of the brown shrimp, *Penaeus aztecus*, has been well documented (Pearson, 1939; Williams, 1955). This life-cycle includes offshore spawning, oceanic larval development, and migration into estuaries as postlarvae. Following rapid growth in the estuary, shrimp return to offshore areas as subadults. While estuaries presumably provide certain conditions necessary for developing postlarval penaeids (Williams, 1959; Gunter, 1961; Weinstein, 1979), the specific contributions of estuarine habitats are not known. One important function, however, may be the provision of abundant and necessary food resources not readily available in offshore areas.

Along the eastern seaboard and Gulf coast, salt marshes are dominated by the smooth cordgrass, *Spartina alterniflora* (Chapman, 1960). These marshes produce an abundance of plant detritus (Odum & De la Cruz, 1967), but its direct importance to the nutrition of penaeid shrimp has not been established. In some studies the nutritional value of detritus and its associated microorganisms has been implied by the presence

of this plant-microbe complex in gut contents (Jones, 1973; George, 1978; Chong & Sasekumar, 1981). Other studies have cast doubt on the nutritional value of detritus because: (1) other plant and animal materials are often abundant in shrimp guts (Moriarty & Barclay, 1981), (2) high concentrations of *Penaeus aztecus* have been found in areas where detrital production is low (Weinstein, 1979), and (3) marsh associated algae may be eaten and better assimilated by penaeids (Hughes & Sherr, 1983). The role of plants in the nutrition of shrimp associated with the *Spartina* habitat has received little attention. Laboratory studies have shown that juvenile penaeids readily feed on various algae including diatoms (Williams, 1958, 1959; Zein-Eldin, 1963; Rickards, 1971; Condrey *et al.*, 1972; Venkataramiah *et al.*, 1975; Brisson & Pace, 1978), and digest and assimilate plant cell walls (Moriarty, 1976). In addition, maximum growth rates have usually been attained when combinations of plant and animal material were fed to shrimp (Williams, 1958; Venkataramiah *et al.*, 1975). The presence of vegetable matter in the diet of shrimp has been suggested to be essential for high survival and efficient energy conversion of protein sources (Venkataramiah *et al.*, 1975).

Based on recent studies demonstrating a strong positive correlation between juvenile shrimp densities and the presence of *S. alterniflora* habitat (Zimmerman *et al.*, 1984), we hypothesized that plant materials associated with *Spartina* might provide an important source of nutrition for growth in developing shrimp. Although this study investigated only the importance of plant materials in the diet of *Penaeus aztecus*, we recognize that postlarval penaeid shrimp may be omnivorous. Research on field populations has indicated a diet consisting of various proportions of plant and animal sources but has not determined the relative importance of each of these components in terms of growth and survival (Condrey *et al.*, 1972; Jones, 1973). By taking postlarvae from the field and rearing these animals on representative salt marsh plant materials, this study represented a first step in partitioning the contribution of each of these food sources to the nutrition of *Penaeus aztecus* Ives.

METHODS AND MATERIALS

All *Penaeus aztecus* postlarvae were captured using a hand-towed beam trawl (Renfro, 1963) either on the front beach or at one of two passes on either end of Galveston Island, Texas. Brown shrimp postlarvae migrating from open coastal waters through the passes averaged 10–12 mm (rostrum–telson) in length. Postlarvae were taken to the laboratory, identified according to Ringo & Zamora (1968) and starved for not < 12 h nor > 24 h before initiation of the experiments.

Four sources of plant material were used in the experiments: *Spartina* detritus, epiphytes of *Spartina*, *Skeletonema costatum* (Greville) Cleve and *Isochrysis* sp. The epiphytic and detrital materials were collected from a *Spartina* marsh located in Galveston Island State Park on the West Bay side of Galveston Island. A complex, termed *Spartina* detritus, of decaying vascular plant fragments and *Aphanothece stagnina*

(Spreng.) A. Br. (a gelatinous colonial blue-green alga) was collected by straining the top 5 cm of sediment from within *Spartina* stands through a 250- μ m sieve. Material carefully scraped with a scalpel from *Spartina* stems was referred to as epiphytes. These epiphytes consisted of many species of green algae, blue-green algae, and colonial diatoms. Common species of each present were *Ulothrix flacca* (Dillw.) Thur. and *U. subflaccida* Wille, *Oscillatoria curviceps* Ag. ex Gomont, and *Nitzschia claustrum* (Ehr.) Wm. Smith, respectively. After removal of visible macrofauna, a meiofaunal component (predominantly nematodes) remained in treatments with detritus and epiphytes (Table I). Preliminary experiments indicated that postlarval *Penaeus aztecus*,

TABLE I

Macrofaunal and meiofaunal abundances in random samples of epiphytic and detrital material before and after being thoroughly washed with filtered (5 μ m) sea water: values represent means with 1 SEM in parentheses; one sample equals 1 ml of plant material; the plant materials remaining after processing were used in the feeding experiments.

	<i>n</i>	Nematodes	Oligochaetes and polychaetes	Copepods
Before processing				
<i>Spartina</i> epiphytes	4	157.5 (16.4)	0.3 (0.3)	9.3 (1.0)
<i>Spartina</i> detritus	4	78.0 (4.5)	4.0 (1.6)	3.0 (1.1)
After processing				
<i>Spartina</i> epiphytes	4	3.0 (0.8)	0.0 (0.0)	0.3 (0.3)
<i>Spartina</i> detritus	4	2.3 (0.5)	0.3 (0.3)	0.0 (0.3)

residing for 4 days in beakers containing detritus, feed on these meiofauna (detritus, mean = 27.5 worms/sample, $n = 10$; detritus + shrimp, mean = 9.8 worms/sample, $n = 10$; $F = 21.59$, d.f. = 1,18, $P < 0.01$ by analysis of variance, ANOVA). To reduce the confounding effects of animal contaminants (Table I), detritus and epiphyte treatments were subjected to a two-step procedure which included (1) thoroughly washing the samples with filtered sea water and (2) allowing the samples to remain undisturbed for a minimum of 48 h. *Skeletonema* (a planktonic diatom) and *Isochrysis* (a flagellated green alga) treatments were available from algal cultures virtually free of contamination except for infrequent dinoflagellates. Thus, differences in growth and survival between treatments were attributed to the ingestion of plant materials and their associated bacteria and fungi.

To prevent cannibalism, postlarvae were reared individually in 250-ml beakers filled with sea water. Growth and survival were assessed in 16 treatments, including all possible combinations of the four plant sources and a starvation treatment. Each treatment was comprised of 10 individually contained shrimp (replicates). The foods were presented to the shrimp in concentrations exceeding that which the postlarvae could consume in a 4-day period. In treatments with *Spartina* epiphytes and *Spartina*

detritus, shrimp were placed with 0.5 ml of plant material in 250 ml of filtered ($5\ \mu\text{m}$) sea water. For *Skeletonema* and *Isochrysis*, initial densities in each 250 ml replicate were $\approx 5 \times 10^5$ cells/ml. Plant materials were replaced and beakers thoroughly cleaned every 4 days to prevent depletion of food resources and microfloral contamination. One-half of the water in each beaker was exchanged every 2 days between plant replacements. Daily observations verified that all food sources were abundant during the entire 16 days. To maintain the treatments containing *Skeletonema*, *Isochrysis*, and *Spartina* epiphytes, 0.5 ml of 2% F/2 algae media (Guillard, 1975) was added initially and at each plant replacement. Preliminary experiments indicated that addition of F/2 algae media had no effect on either growth or survival of the postlarvae. Comparisons between shrimp in the presence and absence of algae media found $P > 0.10$ in length and weight (ANOVA), and $P > 0.25$ in survival (Kruskal-Wallis test).

Shrimp were subjected to a 12 h light/12 h dark photoperiod, and salinity and temperature were maintained at $25 \pm 1\text{‰}$ and $25 \pm 1^\circ\text{C}$ to promote optimal growth (Zein-Eldin, 1963; Zein-Eldin & Aldrich, 1965; Zein-Eldin & Griffith, 1966). To reduce evaporation and prevent shrimp from escaping the beakers, a thin polyethylene cover (plastic wrap) was placed on the surface of the water. Dissolved O_2 was monitored every other day between 0800 and 1200 by sampling 12 beakers (3 each containing *Skeletonema*, *Isochrysis*, detritus, and epiphytes) with a YSI Model 51B oxygen meter. Oxygen concentration in the beakers was never < 5 ppm and in most cases ranged between 8–10 ppm due to photosynthesis.

At 4-day intervals lengths and weights were determined by measuring individual shrimp (rostrum–telson) under a dissecting microscope to the nearest 0.1 mm, blotting dry, and then weighing on a microbalance to the nearest 0.2 mg. Earlier experiments utilizing the same protocol indicated little if any mortality due to the measuring and weighing procedure. Observations on mortality were taken every other day. Initial lengths and weights were not significantly different between treatments (one-way ANOVA; $F = 1.5$, d.f. = 15,144, $P = 0.34$ for length; $F = 1.12$, d.f. = 15,144, $P = 0.11$ for weight).

RESULTS

OBSERVATIONS

In those beakers containing plant material, shrimp moved to the bottom and began active feeding immediately. That all foods were ingested was indicated by the fact that the guts of all postlarvae remained full during the entire experimental period, with the exception of the “no food” treatment. Where substratum was available (i.e. treatments containing *Spartina* epiphytes or detritus) postlarvae were usually found on or burrowed among the plant material. In all other beakers the shrimp were more often observed swimming in the water column.

GROWTH

At the end of the 16-day experiment changes in lengths and weights among survivors were significantly different between treatments (general linear models procedure, SAS Institute Inc., 1982; $F = 10.75$, d.f. = 11,86, $P < 0.0001$ for length; $F = 10.45$, d.f. = 11,86, $P < 0.0001$ for weight). A posteriori comparisons revealed three distinct groups ($P < 0.05$, Duncan's multiple range test) in both length and weight analysis (Table II). Growth of the shrimp within each group was dependent on a principal food source (i.e. *Skeletonema costatum* or *Spartina* epiphytes). The greatest increases in length and weight were attained in *Skeletonema costatum* treatments (*Skeletonema* group) followed by treatments containing *Spartina* epiphytes without *Skeletonema* (epiphyte group) (Table III). Essentially no change occurred among shrimp in *Isochrysis* sp., *Spartina* detritus, or no food (*Isochrysis*-detritus-no food group) treatments (Table

TABLE II

Growth of postlarval *Penaeus aztecus* reared 16 days on various plant materials: values represent means with 1 SEM in parentheses; in all treatments initial $n = 10$; final lengths and weights between the three groups were significantly different by Duncan's multiple range test ($\alpha = 0.05$); Skel, *Skeletonema costatum*; Iso, *Isochrysis* sp.; Epi, *Spartina* epiphytes; Det, *Spartina* detritus.

Treatment	Final <i>n</i>	Percent survival	Mean length (mm)		Mean weight (mg)	
			Initial	Final	Initial	Final
<i>Skeletonema</i> group						
Skel, Iso, Epi, Det	10	100	12.42 (0.11)	14.55 (0.48)	7.8 (0.2)	15.9 (0.8)
Skel, Epi	8	80	12.43 (0.08)	14.64 (0.15)	8.0 (0.2)	16.0 (0.6)
Skel, Epi, Det	6	60	12.54 (0.11)	14.63 (0.53)	8.2 (0.2)	16.4 (1.8)
Skel, Det	7	70	12.34 (0.09)	14.29 (0.30)	7.8 (0.2)	14.6 (1.1)
Skel, Iso	9	90	12.56 (0.10)	14.48 (0.20)	8.6 (0.3)	15.3 (0.7)
Skel	9	90	12.58 (0.12)	14.44 (0.28)	8.5 (0.3)	15.3 (1.1)
Skel, Iso, Epi	10	100	12.58 (0.17)	14.49 (0.19)	8.5 (0.3)	15.1 (0.7)
Skel, Iso, Det	8	80	12.48 (0.14)	14.07 (0.15)	8.2 (0.3)	13.6 (0.5)
Overall mean	8.4	84	12.51 (0.04)	14.46 (0.09)	8.2 (0.1)	15.2 (0.8)
Epiphyte group						
Epi, Iso	6	60	12.51 (0.08)	13.35 (0.03)	8.1 (0.2)	11.4 (0.2)
Epi	8	80	12.83 (0.17)	13.56 (0.22)	9.0 (0.4)	11.8 (0.7)
Epi, Iso, Det	10	100	12.59 (0.13)	13.14 (0.16)	8.3 (0.3)	10.8 (0.4)
Epi, Det	7	70	12.65 (0.15)	13.35 (0.24)	8.7 (0.4)	11.2 (0.7)
Overall mean	7.8	78	12.65 (0.07)	13.36 (0.09)	8.5 (0.2)	11.3 (0.3)
<i>Isochrysis</i> -detritus-no food group						
Iso	0	0	12.22 (0.16)	0	7.6 (0.4)	0
Det	4	40	12.59 (0.16)	12.44 (0.08)	8.5 (0.3)	7.7 (0.5)
Iso, Det	0	0	12.53 (0.15)	0	8.4 (0.3)	0
No food	0	0	12.45 (0.08)	0	8.2 (0.3)	0
Overall mean	1.0	10	12.45 (0.07)	12.44 (0.08)	8.2 (0.2)	7.7 (0.5)

III). These results suggest that the presence of certain plant materials did not have additive or synergistic effects on growth.

Growth of postlarvae in the *Skeletonema* and epiphyte groups accelerated after the first 4 days (Figs. 1, 2). During the initial period postlarvae in *Skeletonema* treatments grew at a rate of 0.03 mm/day and 0.2 mg/day ($n = 74$), and individuals in epiphyte treatments increased at a rate of <0.01 mm/day and 0.05 mg/day ($n = 38$). Following

TABLE III

Changes in lengths and weights and growth rates after 16 days for postlarval *Penaeus aztecus* reared on plant diets: values represent means with 1 SEM in parentheses; see legend Table II for group designations.

Group	Final <i>n</i>	Change in length (mm) (final-initial)	Rate (mm/day)	Change in weight (mg) (final-initial)	Rate (mg/day)
<i>Skeletonema</i>	67	1.95 (0.07)	0.12 (0.01)	7.0 (0.3)	0.4 (0.02)
Epiphyte	31	0.72 (0.08)	0.05 (0.01)	2.8 (0.2)	0.2 (0.01)
<i>Isochrysis</i> - detritus- no food	4	-0.16 (0.06)	-	-0.8 (0.3)	-

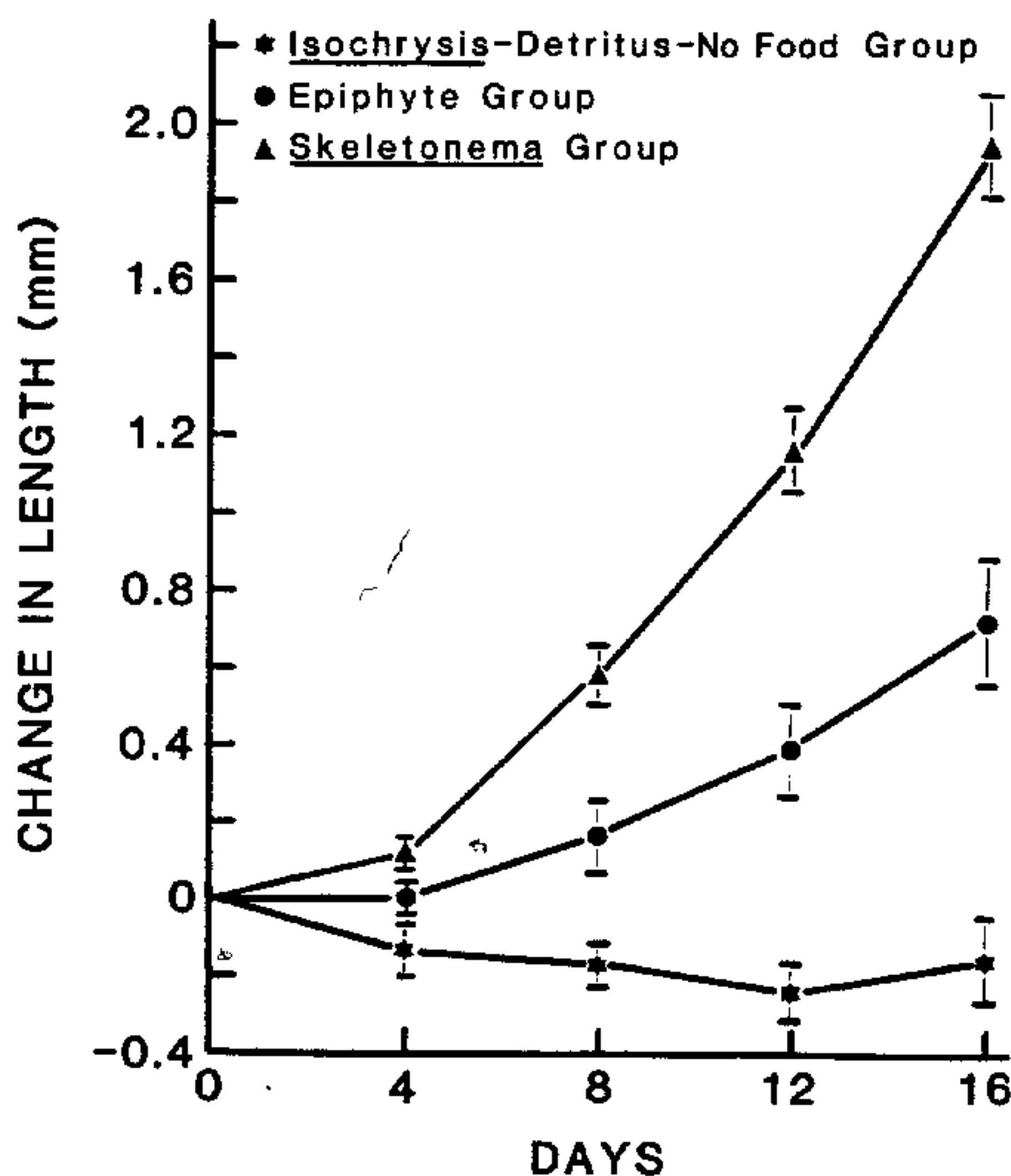


Fig. 1. Changes in length (Day x - initial) for postlarval *Penaeus aztecus* reared 16 days on plant diets: consecutive measurements were taken on all surviving individuals at 4-day intervals; see Table II for group designations; bars denote 95% confidence intervals.

this initial interval growth rates increased to 0.15 mm/day and 0.5 mg/day ($n = 67$) for *Skeletonema* group individuals and 0.06 mm/day and 0.2 mg/day ($n = 31$) for epiphyte group individuals. Changes in length and weight remained essentially linear throughout the final 12 days (Figs. 1, 2). Shrimp in the *Isochrysis*-detritus-no food group exhibited neither significant increases nor decreases in both length and weight during the course of the experiment (Figs. 1, 2).

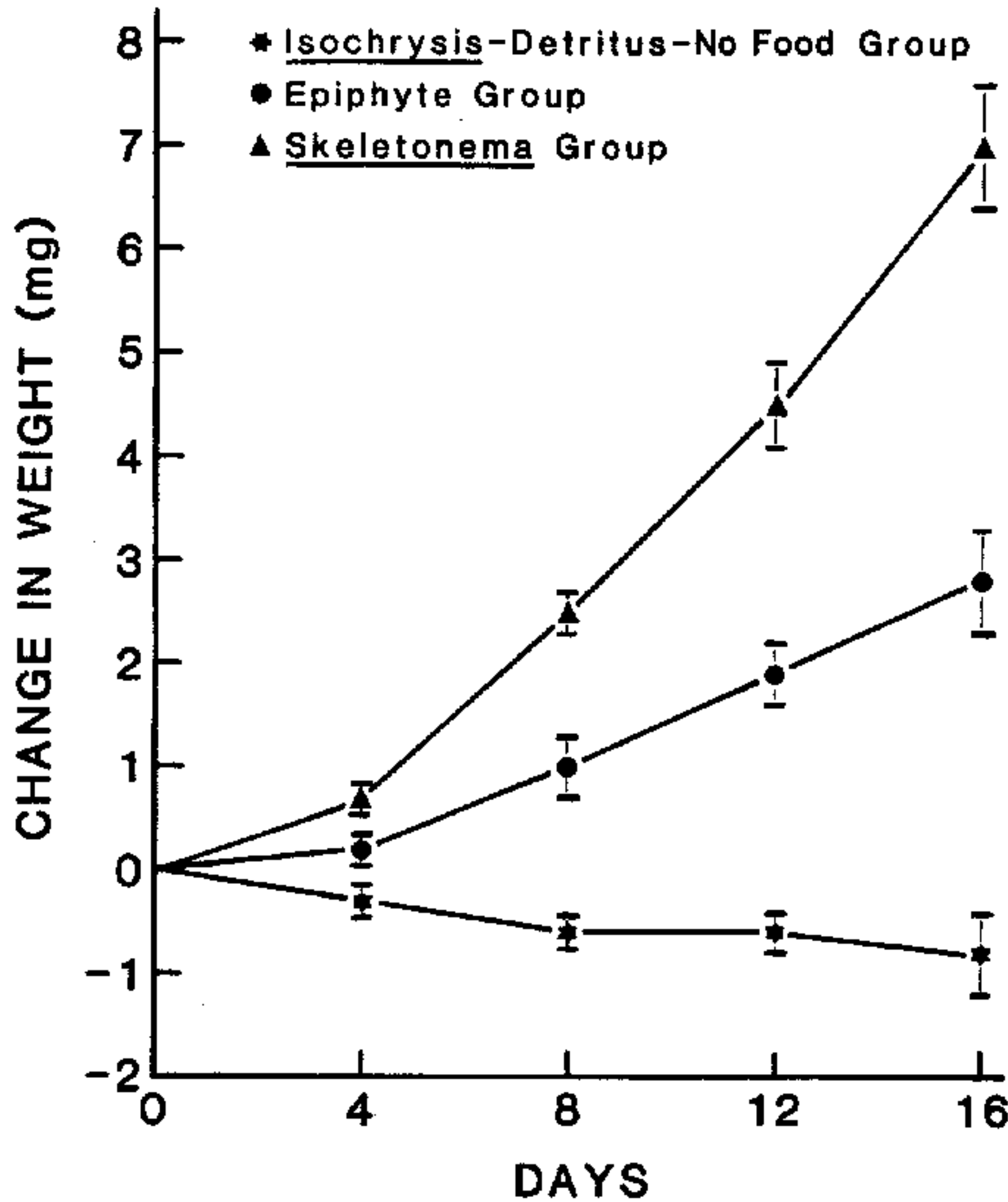


Fig. 2. Changes in weight (Day x - initial) for postlarval *Penaeus aztecus* reared 16 days on plant diets: consecutive weights were taken on all surviving individuals at 4-day intervals; see Table II for group designations; bars denote 95% confidence intervals.

The pattern of change-in-weight versus change-in-length was similar between the *Skeletonema* and epiphyte groups with weight increasing faster than length. Weight increased an average of 4.4 times faster than length in the *Skeletonema* group and 5.0 times faster in the epiphyte group. In addition to length and weight increases, molting occurred. Exuviae were occasionally found, but were rapidly consumed thus restricting monitoring of molting frequencies. Exuviae were also present in *Isochrysis* and *Spartina* detritus treatments throughout the course of the experiments indicating that growth and ecdysis may not be strictly related. Individuals in the *Isochrysis*-detritus-no food group frequently had soft exoskeletons.

SURVIVAL

To test whether it paralleled growth, survival was compared among the *Skeletonema*, epiphyte, and *Isochrysis*-detritus-no food groups. Ranking of all individuals according to the number of days survived indicated significant differences in overall survival (Kruskal-Wallis test, $\chi^2 = 33.24$, d.f. = 2, $n = 160$, $P < 0.0001$). No significant difference in survival, however, was found between the *Skeletonema* and epiphyte groups (Wilcoxon two-sample test, $z = -0.5317$, $P = 0.60$). Therefore, survival was significantly higher in the *Skeletonema* and epiphyte groups as compared to the *Isochrysis*-detritus-no food group.

Survival, after 16 days among treatments in the *Skeletonema* and epiphyte groups, was 60 to 100% (Table II) with mean days survived ranging from 10.6 to 16.0 (Fig. 3). Of mortalities which occurred in the *Skeletonema* and epiphyte groups, many (41%) occurred within the first 4 days. Deaths during this initial period were probably caused

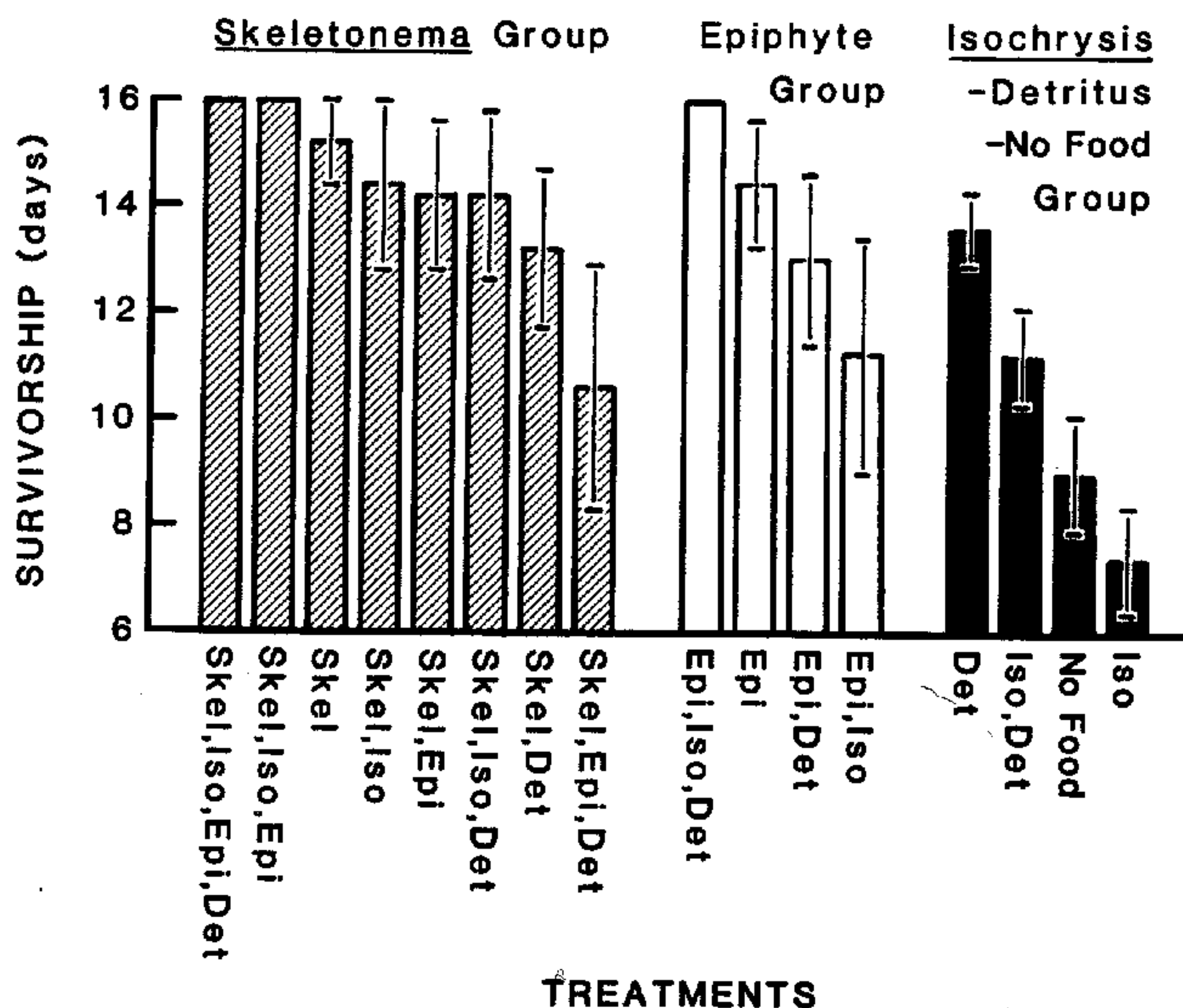


Fig. 3. Days of survival for postlarval *Penaeus aztecus* exposed to all possible combinations of four plant materials: the groupings are based on the results of the growth analyses; means: *Skeletonema* group = 14.2 ± 0.6 SE ($n = 80$); epiphyte group = 13.7 ± 0.8 SE ($n = 40$); *Isochrysis*-detritus-no food group = 10.3 ± 0.6 SE ($n = 40$); survival in the *Skeletonema* and epiphyte groups was significantly higher than in the *Isochrysis*-detritus-no food group (Kruskal-Wallis test and Wilcoxon two-sample test); all bars represent means based on 10 individuals; intervals, where appropriate, represent 1 SEM; Skel, *Skeletonema costatum*; Iso, *Isochrysis* sp.; Epi, *Spartina* epiphytes; Det, *Spartina* detritus.

from injuries or stress resulting from netting, transporting, and handling. Survival in the *Isochrysis*-detritus-no food group was 0% to 40% (Table II) and mean days survived was 7.4 to 13.6 (Fig. 3). Thus, survival paralleled growth patterns with significantly higher survival in the *Skeletonema* and epiphyte groups compared to the *Isochrysis*-detritus-no food group.

Comparisons of survival among treatments containing only single food sources resulted in highly significant differences (Kruskal-Wallis test, $\chi^2 = 18.99$, d.f. = 3, $P < 0.005$). However, excluding *Isochrysis* and testing for differences between *Skeletonema*, epiphytes, and detritus resulted in non-significance (Kruskal-Wallis test, $\chi^2 = 3.09$, d.f. = 2, $P > 0.10$). This indicates that detritus, even without promoting growth, provided the shrimp with nutrients which extended survival beyond the level obtained on *Isochrysis*.

DISCUSSION

Our experiments indicate that postlarval brown shrimp are able to survive and maintain a positive rate of growth for 16 days on diets consisting exclusively of plant material. That diatoms contribute to the natural diet of postlarval shrimp is supported by the increases in length and weight obtained when feeding on *Skeletonema costatum*. The high survival and positive growth rates associated with the *Spartina* epiphytes diet indicates, as suggested by Condrey *et al.* (1972), that this food may be more nutritionally important than previously thought. We have also shown that *Spartina* detritus, the nutritional value of which has been questioned (Jones, 1973; George, 1978; Weinstein, 1979; Chong & Saskemur, 1981; Moriarty & Barclay, 1981), does not promote growth of postlarvae. Overall these results may have substantial relevance to understanding natural shrimp diets considering abundances and availability of algae as food in *Spartina* marshes (Blum, 1968; Lowe & Cox, 1978; Pomeroy *et al.*, 1981).

Although length and weight increases were more rapid in *Skeletonema* than in epiphytes, the overall growth patterns in the two treatments were the same. Diatoms were present in both treatments lending further support to the hypothesis that diatoms are important in the natural diet of postlarval shrimp. *Skeletonema* is a chain-forming planktonic diatom while many of the algae that compose the epiphyte assemblage are branching colonial forms. This hypothesis is further supported by preliminary field caging experiments which displayed rapid growth and high survival of shrimp in treatments which included diatom-rich phytoplankton (Wellington & Gleason, in prep.).

Field studies report growth rates of ≈ 1.1 mm/day (reviewed by Knudsen *et al.*, 1977) while the maximum growth rate achieved with *Skeletonema* in this study was 0.12 mm/day. However, since animal material was not included in our experimental diets and growth measurements in field studies have usually involved older individuals, this is not an appropriate comparison. In addition, laboratory studies have found growth of postlarvae to be slow initially, followed by more rapid increases (Zein-Eldin,

1963; Zein-Eldin & Griffith, 1966; Fry & Arnold, 1982). The ability of shrimp fed plant diets to survive and achieve growth indicates that these materials may provide a maintenance diet during periods in which the appropriate foods, or mix of foods, are not available. This ability of switching to feed on the dominant plant or animal components, has been found to occur in the planktonic copepod *Calanus pacificus* (Landry, 1981). If this feeding mode occurs with postlarval brown shrimp, it would provide a distinct advantage in increased survival.

It is unlikely that *Penaeus aztecus* is a strict herbivore because the growth rates measured in the present study were substantially lower than those reported in previous laboratory studies where postlarval shrimp were fed *Artemia* (Zein-Eldin, 1963; Zein-Eldin & Griffith, 1966; Fry & Arnold, 1982). Detritus may still contribute to nutrition indirectly through postlarval feeding on detritivores. This possibility is supported by preliminary experiments indicating significant reductions in nematode densities when shrimp were present in detritus treatments (see p. 237). While shrimp did not survive on *Spartina* detritus other types of detritus may be nutritionally useful. For example, detritivores such as the polychaete, *Capitella capitata*, and nematode, *Diplolaimella chitwoodi*, assimilate seagrass and algal detritus, to a greater degree than *Spartina* detritus (Findlay, 1982; Findlay & Tenore, 1982).

Molting without growth occurred in detritus and *Isochrysis* treatments, but was absent in the "no food" treatment. Although molting in crustaceans is generally associated with an increase in body volume (Russell-Hunter, 1979), no increases in either length or weight were detected in these treatments. Apparently the stimuli which triggered ecdysis were unrelated to growth.

Neither additive nor synergistic effects occurred when postlarvae were provided with combinations of foods. This suggests either preferential feeding, differential assimilation, or some association between the two. Accordingly, the data imply the following preference-assimilation hierarchy: *Skeletonema costatum* > *Spartina* epiphytes > *Spartina* detritus = *Isochrysis* sp. However, this hierarchy may not result from preferences and assimilation alone, but may also involve foraging times and ingestion rates. Experiments using a similar rearing procedure are beginning to test this hypothesis by assessing assimilation rates through stable carbon isotope tracing. Assuming that the foraging times and ingestion rates are the same for all individuals, then differential assimilation is expected. Preliminary results indicate that this is occurring with the most rapid assimilation rates in shrimp fed *Skeletonema* (Gleason, unpubl.).

Postlarval brown shrimp survived and achieved linear growth on plant sources indicating possible plant contributions in the natural diet. Perhaps algal epiphytes on *Spartina*, especially the colonial diatoms, as suggested by Condrey *et al.* (1972), and planktonic diatoms, such as *Skeletonema*, are important nutritional resources for brown shrimp in marsh ecosystems. Recent field sampling has found *Skeletonema* to be one of the dominant algal species in Galveston marshes with densities up to 1000 cells/ml not uncommon (S.R. Indelicato, pers. comm.). *Spartina* detritus, and its associated epibenthic blue-green algae, however, appear to provide little or no direct source of

nutrition. Preliminary experiments indicate that the resistant gelatinous outer coat in one species of benthic blue-green algae present in the detrital community, *Aphanothece stagnina*, prevents the postlarvae from successfully penetrating and feeding on this plant.

ACKNOWLEDGEMENTS

For technical assistance we thank G. F. R. Marsden and other members of the Texas A&M Larviculture Facility in Galveston, G. R. Zamora, S. R. Indelicato and T. L. Macatee. We also thank T. J. Minello and two anonymous reviewers for improving earlier drafts. In particular, we thank G. M. Wellington for his guidance and support. This work was part of a thesis submitted by D. F. Gleason in partial fulfillment of the requirements for a M. A. degree in the Dept. of Biology, Univ. of Houston, Houston, Texas. Support was provided by the National Marine Fisheries Service-Galveston Laboratory and by the Texas A&M University Sea Grant College Program (R/ES-4).

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